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ACCEPTANCE OF *LOTUS SCOPARIUS* (FABACEAE) BY LARVAE OF LYCAENIDAE

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ABSTRACT. Larvae of 49 species of Lycaenidae were fed *Lotus scoparius* (Nutt. in T. & G.) Ottley (Fabaceae). Twentyseven species grew normally and pupated; six others fed but exhibited retarded development. Sixteen species refused to feed, or fed but exhibited no growth. Fourteen of the species reared to adults on *L. scoparius* are not known to use food plants in the Fabaceae in nature.

Additional key words: coevolution, food plant, host shift.

The larvae of most butterfly genera feed specifically on either a single genus or family of plants (Ehrlich & Raven 1964, Ackery 1988). The host range of some genera of Lycaenidae is comparatively broad. For example, members of the genus *Callophrys* Billberg feed on a wide range of plants in the families Convolvulaceae, Crassulaceae, Cupressaceae, Ericaceae, Fabaceae, Agavaceae, Pinaceae, Polygonaceae, Rhamnaceae, Rosaceae, and Viscaceae (Powell 1968, Emmel & Emmel 1973, Scott 1986, Ballmer & Pratt 1989b). Some lycaenid species, such as *Strymon melinus* Hübner, are also extremely polyphagous, whereas others are monophagous or oligophagous.

One of us (GFP) observed that *Callophrys mcfarlandi* (Ehrlich & Clench) which, in nature, is monophagous on *Nolina texana* var *compacta* (Trel.) (Agavaceae), could be reared in the laboratory on *Lotus scoparius* with little or no retardation in development. This plasticity in larval feeding capacity could indicate a broader ancestral host range and might support the theory that ancestral butterflies fed on Fabaceae (Scott 1984). We tested 48 other Lycaenidae to determine if they would accept *Lotus scoparius* as a larval host.

MATERIALS AND METHODS

Larvae were reared in the laboratory under incandescent lights in screened vials (with two circular screens 2 cm in diameter, one on the side and one on the top) on fresh *Lotus scoparius* kept in water and changed every 3 days, at ca. 25°C as described by Ballmer and Pratt (1989a). *Lotus scoparius* plants were collected in the field at Riverside,

Riverside Co., California. Both leaves and flowers were presented to all larvae tested. Larvae were field collected or reared from ova obtained from captive females. For butterfly species with no feeding or in which feeding was retarded on *L. scoparius,* often we had a subsample of larvae from that population being reared on its natural host.

The origins of tested organisms are as follows (numbers of larvae tested in parentheses): *Apodemia mormo* (C. and R. Felder) *ex* ova *Eriogonum inflatum* Torr. & Frem. (Polygonaceae) (6), Sheephole Pass, San Bernardino Co., California, April 1988; *Lycaena cupreus* (W. H. Edwards) *ex* female (2), Tioga Pass, Inyo Co., California, July 1987; *L. gorgon* (Boisduval) *ex* female (2), Butterbread Peak, Kern Co., California, June 1986; *L. hermes* (W. H. Edwards) *ex* female (2), Guatay, San Diego Co., California; *L. heteronea* (Boisduval) *ex* female (2), Mt Bidwell, Modoc Co., California, July 1986; *L. nivalis* (Boisduval) *ex* female (2), Sonora Pass, Mono Co., California, July 1987; *L. phlaeas* (Linnaeus) *ex* female (3), White Mt, Inyo Co., California, July 1987; *L. xanthoides* (Boisduval) *ex* larvae on *Rumex crispus* L. (Polygonaceae) (2), Mojave River Forks, San Bernardino Co., California, April 1987; *Atlides halesus* (Cramer) *ex* ova on *Phoradendron tomentosum* (Englm. ex Gray) (Viscaceae) (2), Riverside, Riverside Co., California, May 1988; *Callophrys augustus* (W. Kirby) *ex* larvae on *Ceanothus* (Rhamnaceae) (2), San Bernardino Mts, San Bernardino Co., California, May 1988; *C. eryphon* (Boisduval) *ex* female (3), San Bernardino Mts, San Bernardino Co., California, June 1988; *C. fotis* (Strecker) *ex* larvae on *Cowania mexicana* D. Don (Rosaceae) (3), Providence Mts, San Bernardino Co., California, May 1988; *C. mossii* (Hy. Edwards) *ex* larvae on *Sedum spathulifolium* Hook. (Crassulaceae) (10), San Bernardino Mts, San Bernardino Co., California, May 1988; *C. perplexa* Barnes and Benjamin *ex* female (3), San Bernardino Mts, San Bernardino Co., California, May 1988; *C. polios* (Cook & Watson) *ex* female (20), Del Norte Co., California, April 1990; *C. siva* (W. H. Edwards) *ex* female (6), Barnwell, San Bernardino Co., California, May 1988; *C. spinetorum* (Hewitson) *ex* ova on *Arceuthobium campylopodum* Engelm. in Gray (Viscaceae) (2), Laguna Mts, San Diego Co., California, June 1988; *C. mcfarlandi ex* larvae on *Nolina texana* var *compacta* (Trel.) (Agavaceae) (6), San Augustin Pass, New Mexico, April, 1987; *Erora guaderna ex* female (6), Santa Rita Mts, Arizona, March 1987; *Chlorostrymon simaethis* (Drury) *ex* larvae (10), 6 mi W. Santa Rita, B. C. S., Mex, April 1991; *Habrodais grunus* (Boisduval) *ex* larvae on *Quercus chrysolepis* Liebm. (Fagaceae) (2), San Bernardino Mts, California, May 1988; *Ministrymon leda* (W. H. Edwards) *ex* female (3), Julian, California, April 1988; *Satyrium auretorum* (Boisduval) ova *ex* female (3), Guatay, California, June 1986; Frazier Park, California, May 1987; *Satyrium behrii* (W. H. Edwards) *ex* larvae on *Purshia glandulosa* Curran (Rosaceae) (3), Isabella Lake, California, May 1987; *Satyrium saepium* (Boisduval) ova *ex* female (2), Guatay, San Diego Co., California, June 1987; *Satyrium tetra* (W. H. Edwards) *ex* larvae on *Cercocarpus betuloides* Nutt. *ex* T. & G. (Rosaceae) (3), San Bernardino Mts, San Bernardino Co., California, May 1988; *Strymon columella* (Fabricius) *ex* female (2), 6 mi. S. San Agustin, B. C., Mex, April 1991; *S. melinus* (Hubner) *ex* female (2), Riverside, Riverside Co., California, May 1988; *Brephidium exilis* (Boisduval) *ex* ova on *Sesuvium verrucosum* Raf. (Aizoaceae) (3), Cronese Dry Lake, San Bernardino Co., California, April 1987; *Brephidium pseudofea* (Morrison) *ex* larvae on *Salicornia* L. (Chenopodiaceae) (2), Florida, July 1987; *Celastrina argiolus* (Linnaeus) *ex* female (6), Santa Rita Mts, Cochise Co., Arizona, March 1987; *Celastrina neglectamajor ex* ova on *Cemicifuga* (Ranunculaceae), State Game Lands #157, Bucks Co., PA, May 1988; *Euphilotes battoides* (Behr) *ex* female (3), Coxey Meadow, San Bernardino Co., California, May 1988; *Euphilotes mojave* (Watson and W. P. Comstock) *ex* ova on *Eriogonum pusillum* T. & G. (Polygonaceae) (3), Mojave River Forks, San Bernardino Co., California, April 1987; *Everes comyntas* (Godart) *ex* female (6), Bakersfield, Kern Co., California, *May 1987; Everes amyntula* (Boisduval) *ex* larvae on *Astragalus lentiginosus* Dougl. (Fabaceae), Coyote Ridge, Inyo Co., California, July 1987; *Glaucopsyche lygdamus* (Doublday) *ex* larvae on *Lotus Scoparius* (Fabaceae) (3), Mojave River Forks, San Bernardino Co., California, April 1985; *Glaucopsyche piasus* (Boisduval) *ex* ova on *Lupinus excubitus* Jones (Fabaceae) (>50), Nine Mile Canyon, Inyo Co., California, May 1988; *Icaricia acmon texana* (Goodpasture) *ex* female (20), San Augustin Pass, New Mexico, April 1987; *Icaricia icarioides* (Boisduval) *ex* ova on *Lupinus* (Fabaceae) (postdiapause larvae tested) (3), Crooked Creek Road, White Mts, Inyo Co., California, August 1987; *Icaricia lupini* (Boisduval) *ex* female (3), Pinyon Mt, Kern Co., California, April 1987; *Icaricia neurona* (Skinner) *ex* female (3), Pinyon Mt, Kern Co., California, April 1987; *Leptotes marina* (Reakirt) *ex* ova on *Amorpha fruticosa* L. (Fabaceae) (2), San Bernardino Mts, San Bernardino Co., California, June 1988; *Lycaeides idas* (Linnaeus) *ex* female (3), Warner Mts, Modoc Co., California, July 1986; *Lycaeides melissa* (W. H. Edwards) *ex* female (3), Mojave River Forks, San Bernardino Co., California, May 1987; *Philotes sonorensis* (C. and R. Felder) *ex* larvae on *Dudleya lanceolata* (Nutt.) Britt. & Rose (Crasulaceae) (3), San Bernardino Mts, San Bernardino Co., California, April 1988; *Philotiella speciosa* (Hy. Edwards) *ex* larvae on *Eriogonum reniforme* Torr. & Frem. (Polygonaceae) (1), In Ko Pah Gorge, Imperial Co., California, April 1988; *Plebejus saepiolus* (Boisduval) *ex* female (3), San Bernardino Mts, San Bernardino Co., California, July 1987; *Plebulina emigdionis* (F. Grinnell) *ex* larvae on *Atriplex canescens* (Pursh) Nutt. (Chenopodaceae) (4), Mojave River, San Bernardino Co., California, May 1987.

RESULTS

Although none of the 49 species of Lycaenidae tested (Table 1) are monophagous on *Lotus scoparius*, species (*Callophrys perplexa*, *Glaucopsyche lygdamus*, *Icaricia acmon*, *Leptotes marina*, and *Strymon melinus*) use it as a larval food plant (Ballmer & Pratt 1989b). Of the 14 tested species whose natural hosts include various Fabaceae, nine feed on Fabaceae exclusively (Table 2). Two of the latter, *Icaricia icarioides* and *Glaucopsyche piasus*, failed to develop on *L. scoparius;* both are specific to *Lupinus* (Table 2). None of the other lycaenids tested are specific to *Lupinus*.

Ten species tested feed on *Eriogonum* in nature; two of these also feed on Fabaceae. Of the eight *Eriogonum* feeding species that do not feed on Fabaceae, six (*A. mormo*, *E. battoides*, *E. mojave*, *I. lupini*, *I. neurona*, and *P. speciosa*) showed some development on *L. scoparius*. The two that did not feed on *Lotus* were *L. gorgon* (Boisduval) and *L. heteronea* (Boisduval). No species of the subfamily Lycaeninae is known to feed on species of Fabaceae.

Larvae of 16 species failed to develop on *L. scoparius* (Table 1). All of these are host-specific to a single species or genus of plants (Table 2). All seven Lycaeninae species tested refused to feed on *Lotus*. Although most Lycaeninae feed on Polygonaceae, one species tested, *L. hermes*, feeds on *Rhamnus crocea* Nutt. in T. & G. (Rhamnaceae) (Comstock & Dammers 1935, Ballmer & Pratt 1989b).

There was variation in the rate of feeding and survival among the butterfly species that fed on *Lotus scoparius*. Although both *Euphilotes* species and *P. speciosa* pupated, none formed an adult, and all three species took at least twice as long to develop as they did on their natural host. Of the two *S. saepium* larvae, one died, the other pupated. Only

TABLE 1. Feeding responses of larvae of different Lycaenidae to *Lotus scoparius*.

Species	Feeding response*	Species	Feeding response
Apodemia mormo	+ (A)	*S. tetra*	−
Lycaena cupreus	−	*Strymon columella*	+ (A)
L. gorgon	−	*S. melinus*	+ (A)
L. hermes	−	*Brephidium exilis*	+ (A)
L. heteronea	−	*B. pseudofea*	−
L. nivalis	−	*Celastrina neglectamajor*	+ (A)
L. phlaeas	−	*C. argiolus cinerea*	+ (A)
L. xanthoides	−	*Euphilotes battoides*	+, − (P)
Atlides halesus	−	*E. mojave*	+, − (P)
Callophrys augustus	+ (A)	*Everes comyntas*	+ (A)
C. eryphon	+ (A)	*E. amyntula*	+ (A)
C. fotis	+ (A)	*Glaucopsyche lygdamus*	+ (A)
C. mossii	+, − (P)	*G. piasus*	−
C. perplexa	+ (A)	*Icaricia acmon texana*	+ (A)
C. polios	+ (A)	*I. icariodes*	−
C. siva	−	*I. lupini*	+ (A)
C. spinetorum	+ (A)	*I. neurona*	+ (A)
C. mcfarlandi	+ (A)	*Leptotes marina*	+ (A)
Chlorostrymon simaethis	+ (A)	*Lycaeides idas*	+ (A)
Erora guaderna	+ (A)	*L. melissa*	+ (A)
Habrodais grunus	−	*Philotes sonorensis*	−
Ministrymon leda	+ (A)	*Philotiella speciosa*	+, − (P)
Satyrium auretorum	+ (A)	*Plebejus saepiolus*	+ (A)
S. behrii	+, − (3rd)	*Plebulina emigdionis*	−
S. saepium	+, − (A)		

* Feeding response: + = fed, development was normal, and pupated (P) (these species diapause as pupae) or later formed an adult (A); +, − = development was retarded compared to controls on natal food plant either formed a small adult (A), pupated (P), or developed to the third instar (3rd); − = refused to feed and died.

one of ten *C. mossii* larvae pupated and it grew slowly. All three *S. behrii* larvae fed on *Lotus scoparius* flowers, but did not grow. Fifty percent of the 20 *C. polios* survived to pupation, yet only one pupa formed an adult. The remaining species exhibited larval development times and percent survival on *L. scoparius* similar to those of larvae reared on their natural host.

The Lycaenidae tested can be divided into four classes depending on the plant parts on which the larvae feed: flowers; flowers and fruits; flowers, fruits, and leaves; and leaves (Table 2). Only two species feed exclusively on flowers in nature: *C. fotis* and *S. behrii*. Six species feed on flowers and fruits: *C. augustus*, *C. mcfarlandi*, *E. battoides*, *E. mojave*, *G. piasus*, and *E. amyntula*. Of these eight flower and flower/fruit feeding species only *S. behrii* and *G. piasus* did not feed or develop on *L. scoparius*. Of the sixteen species that feed exclusively on leaves in nature, only two developed on *L. scoparius: C. eryphon* and *C. spinetorum*. Of the remaining 25 species, which feed either on all parts

TABLE 2. Feeding behaviors of 49 Lycaenidae natural larval food plants.

	Food plant families	Food plant genera	Feeding observations		
			Fl	Fr	Le
Apodemia mormo	Po	Er, Ox	++	++	++
Lycaena					
cupreus	Po	Ru	–	–	++
gorgon	Po	Er	–	–	++
hermes	Rh	Rh	–	–	++
heteronea	Po	Er	–	–	++
nivalis	po	Po	–	–	++
phlaeas	Po	Ru, Oy	–	–	++
xanthoides	Po	Ru	+	–	++
Atlides halesus	Vi	Ph	–	–	++
Callophrys					
augustus	Rh, Ro, Er	2	++	++	–
eryphon	Pi	Pi	–	–	++
fotis	Ro	Co	++	–	–
mossi	Cr	Se	++	++	++
perplexa	Po, Fa	Er, Lo	++	++	++
polios	Er	Ao	++	–	++
siva	Cu	Ju	–	–	++
spinetorum	Vi	Ar	–	–	++
mcfarlandi	Ag	No	++	++	–
Chlorostrymon simaethis	Sa	Ca	++	++	++
Erora quaderna	Rh, Fg	Ce, Qu	++	++	++
Habrodais grunus	Fg	Qu	–	–	++
Ministrymon leda	Fa	Pr	++	–	+
Satyrium					
auretorum	Fg	Qu	++	–	++
behrii	Ro	Pu	++	–	–
saepium	Rh	Ce	–	–	++
tetra	Ro	Cr	–	–	++
Strymon					
columella	Ma	2	++	++	++
melinus	1	2	++	++	++
Brephidium					
exilis	Az, Ch	Ss, At, Ch	++	–	++
pseudofea	Ch	Sa	–	–	++
Celastrina					
argiolus	Ro, Rh, Fa	2	++	++	++
*neglectamajor**	Rn	Cm	++	++	+
Euphilotes					
battoides	Po	Er	++	++	–
mojave	Po	Er	++	++	–
Everes					
comyntas	Fa	Lo	++	+	++
amyntula	Fa	As	++	++	–

TABLE 2. Continued.

	Food plant families	Food plant genera	Feeding observations Fl	Fr	Le
Glaucopsyche					
lygdamus	Fa	Lo, As	++	++	++
piasus	Fa	Lu	++	++	−
Icaricia					
acmon	Po, Fa	Lo, Er	++	++	++
icarioides	Fa	Lu	−	−	++
lupini	Po	Er	++	−	++
neurona	Po	Er	++	−	++
Leptotes marina	Fa, Pl	Lo, Am, Me, Pl	++	++	++
Lycaeides					
idas	Fa	Lo, Lu	+	−	++
melissa	Fa	Lo, Lu	+	−	++
Philotes sonorensis	Cr	Du	++	++	++
Philotiella speciosa	Po	Er, Ox	++	++	++
Plebejus saepiolus	Fa	Tr	++	+	++
Plebulina emigdionis	Ch	At	−	−	++

Plant families are as follows: 1 = many different plant families, Ag = Agavaceae, Az = Aizoaceae, Ch = Chenopodiaceae, Cr = Crassulaceae, Cu = Cupressaceae, Er = Ericaceae, Fa = Fabaceae, Fg = Fagaceae, Ma = Malvaceae, Pi = Pinaceae, Pl = Plumbaginaceae, Po = Polygonaceae, Rh = Rhamnaceae, Ro = Rosaceae, Rn = Ranunculaceae, Sa = Sapindaceae, Vi = Viscaceae.

Plant genera are as follows: 2 = many different plant genera, Am = *Amorpha*, Ao = *Arctostaphylos*, Ar = *Arceuthobium*, As = *Astragalus*, At = *Atriplex*, Ca = *Cardiospermum*, Ce = *Ceanothus*, Ch = *Chenopodium*, Cm = *Cimicifuga*, Co = *Cowania*, Cr = *Cercocarpus*, Du = *Dudleya*, Er = *Eriogonum*, Ju = *Juniperus*, Lo = *Lotus*, Lu = *Lupinus*, Me = *Medicago*, No = *Nolina*, Ox = *Oxytheca*, Oy = *Oxyria*, Ph = *Phoradendron*, Pi = *Pinus*, Pl = *Plumbago*, Po = *Polygonum*, Pu = *Purshia*, Qu = *Quercus*, Rh = *Rhamnus*, Ru = *Rumex*, Sa = *Salicornia*, Se = *Sedum*, Ss = *Sesuvium*, Tr = *Trifolium*.

Feeding observations are as follows: Fl = flowers, Se = seeds, Le = leaves or stems; − = no feeding has been observed; + = some feeding has been observed in either the laboratory or the field, but rarely; ++ = much feeding has been observed.

* The food plant for this species was reported by David M. Wright (pers. comm.).

of the plants or on both flowers and leaves, only two species did not develop on *Lotus: L. xanthoides* and *P. sonorensis*. Only once have we observed *Lycaena xanthoides* feeding on flowers of *Rumex crispus*.

DISCUSSION

Larvae were reared on cuttings of *Lotus scoparius* that were in advanced stages of blooming. At this stage in the plant's development new leaves are not being produced. Lycaenid larvae that feed on leaves generally are adapted to young leaves and shoots (Pratt & Ballmer, unpublished). Larvae of *Glaucopsyche lygdamus* and *Callophrys perplexa* will feed on young leaves of *Lotus scoparius*, both in the laboratory and the field. The adaptation to feeding on young shoots may be due to seasonal changes in the nutritional quality of leaves, as the amount of available nitrogen generally decreases with age (Strong et al. 1984). Therefore it was not surprising that most of the lycaenid larvae tested would not feed on the older vegetation (leaves) of *Lotus scoparius*. The only exception was *Apodemia mormo* larvae, which often have been observed feeding on the older vegetation of their food plant, *Eriogonum inflatum*.

Leaves and seeds often contain toxic compounds, such as cyanogenic glycosides in *Lotus corniculatus* L. (Scriber 1978). Pollen (a major nutritive resource in flowers) of plant species that have mutualistic associations with bees may not have these compounds. The reason for this possible absence of toxic compounds is that pollen is the indirect source of food for the larval development of bees (Weaver & Kuiken 1954). There is a remarkable similarity in the amino acid contents of pollen from diverse species of plants and royal jelly (Weaver & Kuiken 1954). Yet plants differ in their nutritive value and attractiveness to *Apis mellifera* L. (Hymenoptera). In a test of six bee pollinated plant species in six different families, Campana & Moeller (1977) reported sweet clover *Melilotus* sp. (Fabaceae) to be highest in preference and in contribution to brood production.

Of the 31 species observed to feed on flowers at some stage during their larval development, only 4 (12%) did not mature to the pupal stage when reared on the flowers of *L. scoparius*; these were *Satyrium behrii, Glaucopsyche piasus, Philotes sonorensis,* and *Lycaena xanthoides*. It is surprising that neither *S. behrii* nor *G. piasus* developed on the flowers of *Lotus,* as both species feed specifically on pollen of their food plants. The food plant of *Satyrium behrii, Purshia glandulosa,* is closely related to *Cowania mexicana,* the food plant for *Callophrys fotis*. Yet *C. fotis* did quite well on *Lotus* flowers. *Glaucopsyche piasus* is adapted to flowers of another genus of Fabaceae, yet did not develop on *Lotus*.

If the pollens of different species of plants are very similar in nutrition and composition, perhaps the adaptation to feeding on flowers at some stage in the larval development would make larvae capable of feeding on flowers of a large variety of plants. Because first instar larvae are limited in their ability to disperse in search of food, ovipositional mistakes (on flowers) by females of monophagous flower-feeding species may be less costly than those by monophagous leaf-feeding species. This could be extremely important in the historical evolution of host shifts in the Lycaenidae.

Sixteen of the 49 species in this study do not feed on flowers in nature. Of those 16 species, only two, *Callophrys eryphon* and *Callophrys spinetorum*, developed normally on the flowers of *Lotus scoparius*. Since many *Callophrys* species feed on flowers at some stage during their larval development, perhaps these two species have retained the ancestral ability to feed on flowers. In general, larvae of *Callophrys* species are adapted to a wide variety of plants, even though many of them are monophagous or oligophagous. Perhaps this group evolved from a somewhat polyphagous flower- or leaf-feeding species. Only one *Callophrys* species (*C. siva*) did not develop on *Lotus scoparius* flowers.

Of the 16 species that did not complete larval development on *Lotus* flowers, all are specific either to a single host genus or species. For instance, *Lycaena gorgon* and *Lycaena heteronea*, both of which feed on *Eriogonum* (Polygonaceae), do not develop on *Rumex crispus*, another member of Polygonaceae, and feed on it only for short periods; by contrast *L. xanthoides*, which feeds on *Rumex* species, will not even feed on *Eriogonum* (Pratt unpubl. data).

The results presented here do not support Fabaceae as the primitive larval host for the Lycaenidae. Instead, our results indicate that the ability of lycaenids to feed on *L. scoparius* may be correlated more with flower- and fruit-feeding habits than with natural utilization of other members of Fabaceae. Perhaps part of the reason that legumes are fed on by a wide variety of Lycaenidae is that legumes are often high in nitrogenous compounds due to their association with nitrifying bacteria (Pierce 1985).

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